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CHROMOSOMES OF TEN SPECIES OF PHILIPPINE FRUIT BATS (CHIROPTERA: PTEROPODIDAE)

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Abstract.—Standard karyotypes and silver-stained nucleolar organizer regions (Ag-NORs) of ten species of Philippine pteropodids are described. Results are discussed in the context of an updated version of Andersen's (1912) phylogeny. Data for *Cynopterus brachyotis* (2N = 34), *Eonycteris spelaea* (2N = 36) and *Macroglossus minimus* (2N = 34) agree with previous reports. *Pteropus hypomelanus* (2N = 38) and *Rousettus amplexicaudatus* (2N = 36) have standard karyotypes identical to those of congeners. The Philippine endemic species *Haplonycteris fischeri* (2N = 58), *Ptenochirus jagori* (2N = 44) and *Ptenochirus minor* (2N = 46) have distinctive karyotypes consisting primarily of acrocentric elements. *Haplonycteris* has the highest diploid number for the suborder. The karyotypes of *Harpyionycteris whiteheadi* (2N = 36) and *Nyctimene rabori* (2N = 38) are distinctive, but share some apparenntly derived features with cynopterine genera. In all taxa examined, the Ag-NORs corresponded to the secondary constrictions on the pair of "marker" chromosomes. These results demonstrate that the cynopterine section is the most chromosomally variable clade in the Pteropodidae.

The family Pteropodidae is a large and diverse assemblage of Old World bats that appears to constitute a natural group distinct from other chiropterans (Smith 1980, Koopman 1984). In the only monographic study of the entire family, Andersen (1912) used morphological criteria to construct a detailed phylogeny. Andersen's work remains the most complete statement of relationships within the family. However, it is important to test and, if necessary, modify his kinship hypotheses using independent evidence.

Prior analysis of standard karyotypes of pteropodids had led to the early assumption that chromosomal variation within the family is relatively limited (Haiduk et al. 1980). However, differential staining techniques have shown that several genera with similar standard karyotypes substantially differ in banding patterns (Haiduk et al. 1981). Nevertheless, fewer than half of the recognized pteropodid genera have been karyotyped to date, and fewer have been examined for banding patterns (Haiduk et al. 1981).

In this paper, we present standard karyotypes of ten species of Philippine pteropodids representing nine genera and two subfamilies. Chromosomal data for the genera *Haplonycteris, Harpyionycteris, Nyctimene,* and *Ptenochirus,* and for eight of the species are reported for the first time. We also present results on silver-stained nucleolar organizer regions (Ag-NORs) for each species and discuss variation in pteropodid "marker" chromosomes. We have interpreted our results in the context of Andersen's (1912) phylogeny, as updated to include genera described since 1912.

Materials and methods.—Our animals were all freshly collected from wild populations and killed with sodium pentabarbitol (Nembutal) or with chloroform within 24 h of capture. Chromosome terminology and preparation methods followed those of Patton (1967) with the exception that 0.4% potassium chloride was used for the hypo-

tonic treatment. Cells were processed and fixed in the field, and suspensions were stored at 0–10°C within two weeks of fixation. After three to seven months, air-dried slides were made at the University of Utah. Standard karyotypes were prepared for each specimen from photographs of slides stained with Giemsa. Silver-stained nucleolar organizer regions (Ag-NORs) were examined using a procedure modified from that described by Howell & Black (1980). Determinations of diploid number were based on minimal counts of 10 mitotic spreads per individual. Fundamental numbers (FN) refer to numbers of autosomal arms. Due to variable specimen quality and the presence of minute chromosomes in some species, we consider some FN values to be provisional, as indicated by question marks. Specimens examined were prepared as skins with partial skeletons or preserved in fluid and are deposited in the National Museum of Natural History (USNM), Washington, D.C.

Specimens Examined

Cynopterus brachyotis (Muller, 1838).—Leyte Island, Leyte Province, 7 km N Baybay, elev. 10 m, 10°45′N, 124°47′E (1 ♀); Negros Island, Negros Oriental Province, Dumaguete City, elev. 5 m, 09°18′N, 123°18′E (1 ♂, 2 ♀♀).

Eonycteris spelaea (Dobson, 1871).—Leyte Island, Leyte Province, Cathedral Cave, 4 km S, 1 km E Inopacan, elev. 50 m, 10°28′N, 124°45′E (2 ♀♀); Negros Island, Negros Oriental Province, Caves at 4 km N Manjuyod, elev. 20 m, 09°43′N, 123°10′E (4 ♂♂).

Haplonycteris fischeri Lawrence, 1939.—Biliran Island, Leyte Province, 5 km N, 10 km E Naval, elev. 850 m, 11°36′N, 124°29′E (1 ♂, 1 ♀); Leyte Island, Leyte Province, Mount Pangasugan, 10.5 km N, 4 km E Baybay, elev. 700 m, 10°47′N, 124°50′E (1 ♂, 1 ♀).

Harpyionycteris whiteheadi Thomas, 1896.—Leyte Island, Leyte Province, Mount Pangasugan, 10.5 km N, 4 km E Baybay, elev. 700 m, 10°47′N, 124°50′E (3 ♂♂, 4 ♀♀); Negros Island, Negros Oriental Province, Mount Guinsayawan, 3 km N, 17 km W Dumaguete City, elev. 1280 m, 09°22′N, 123°09′E (1 ♀).

Macroglossus minimus (E. Geoffroy, 1810).—Negros Island, Negros Oriental Province, Dumaguete City, elev. 5 m, 09°18′N, 123°18′E (3 ♂♂, 1 ♀).

Nyctimene rabori Heaney & Peterson, 1984.—Negros Island, Negros Oriental Province, Mount Guinsayawan, 3 km N, 17 km W Dumaguete City, elev. 1280 m, 09°22′N, 123°09′E (1 ♂).

Ptenochirus jagori (Peters, 1861).—Leyte Island, Leyte Province, 7 km N Baybay, elev. 10 m, 10°45′N, 124°47′E (1 ♂, 6 ♀♀), Mount Pangasugan, 10.2 km N, 2.2 km E Baybay, elev. 320 m, 10°46′N, 124°49′E (1 ♂).

Ptenochirus minor Yoshiyuki, 1979.—Leyte Island, Leyte Province, Mount Pangasugan, 10.2 km N, 2.2 km E Baybay, elev. 320 m, 10°46′N, 124°49′E (2 ♂♂, 5 ♀♀).

Pteropus hypomelanus Temminck, 1853.—Negros Island, Negros Oriental Province, 9 km N, 14 km W Dumaguete City, elev. 600 m, 09°23′N, 123°11′E (1 ♂, 2 ♀♀).

Rousettus amplexicaudatus (E. Geoffroy, 1810).—Leyte Island, Leyte Province, 7 km N Baybay, elev. 10 m, 10°45′N, 124°47′E (2 ♂♂, 4 ♀♀); Negros Island, Negros Oriental Province, Dumaguete City, elev. 5 m, 09°18′N, 123°18′E (2 ♀♀).

Results

We present standard karyotypes and silver-stained marker chromosomes for male specimens of eight pteropodid species in Figs. 1–4 and briefly discuss them below. Karyotypes for two additional species are discussed, but not illustrated.

Subfamily Pteropodinae

Cynopterus brachyotis. 2N = 34, FN = 58, Fig. 1A.—The karyotype is indistin-

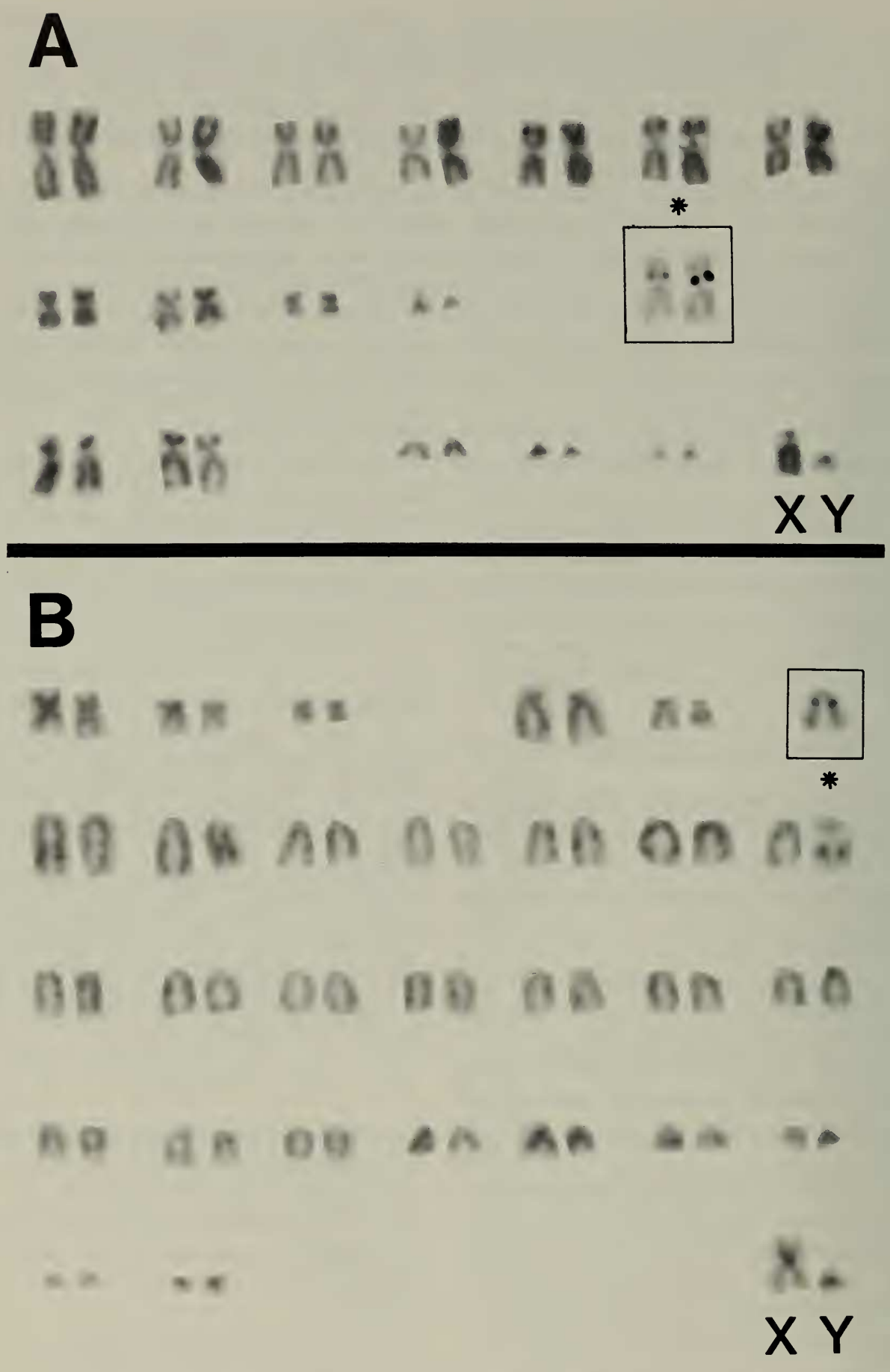

Fig. 1. Standard karyotypes and silver-stained marker chromosomes showing nucleolar organizer regions (insets) of (A) *Cynopterus brachyotis* ♂ (USNM 458083), 2N = 34, FN = 58; (B) *Haplonycteris fischeri* ♂ (USNM 458196), 2N = 58, FN = 66(?).

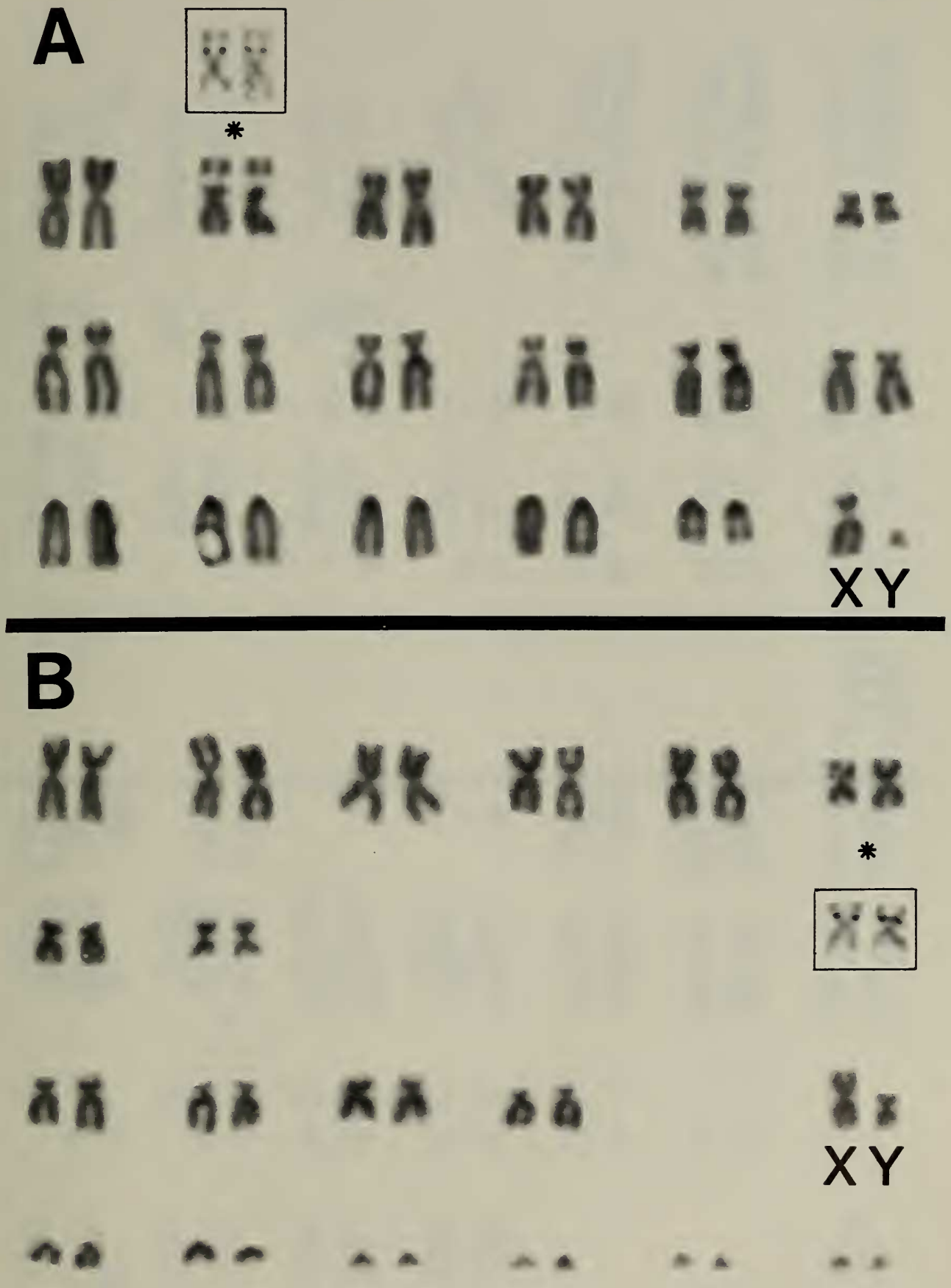

Fig. 2. Standard karyotypes and Ag-NORs (insets) of (A) *Harpyionycteris whiteheadi* ♂ (USNM 458213), 2N = 36, FN = 58; (B) *Nyctimene rabori* ♂ (USNM 458906), 2N = 38; FN = 60.

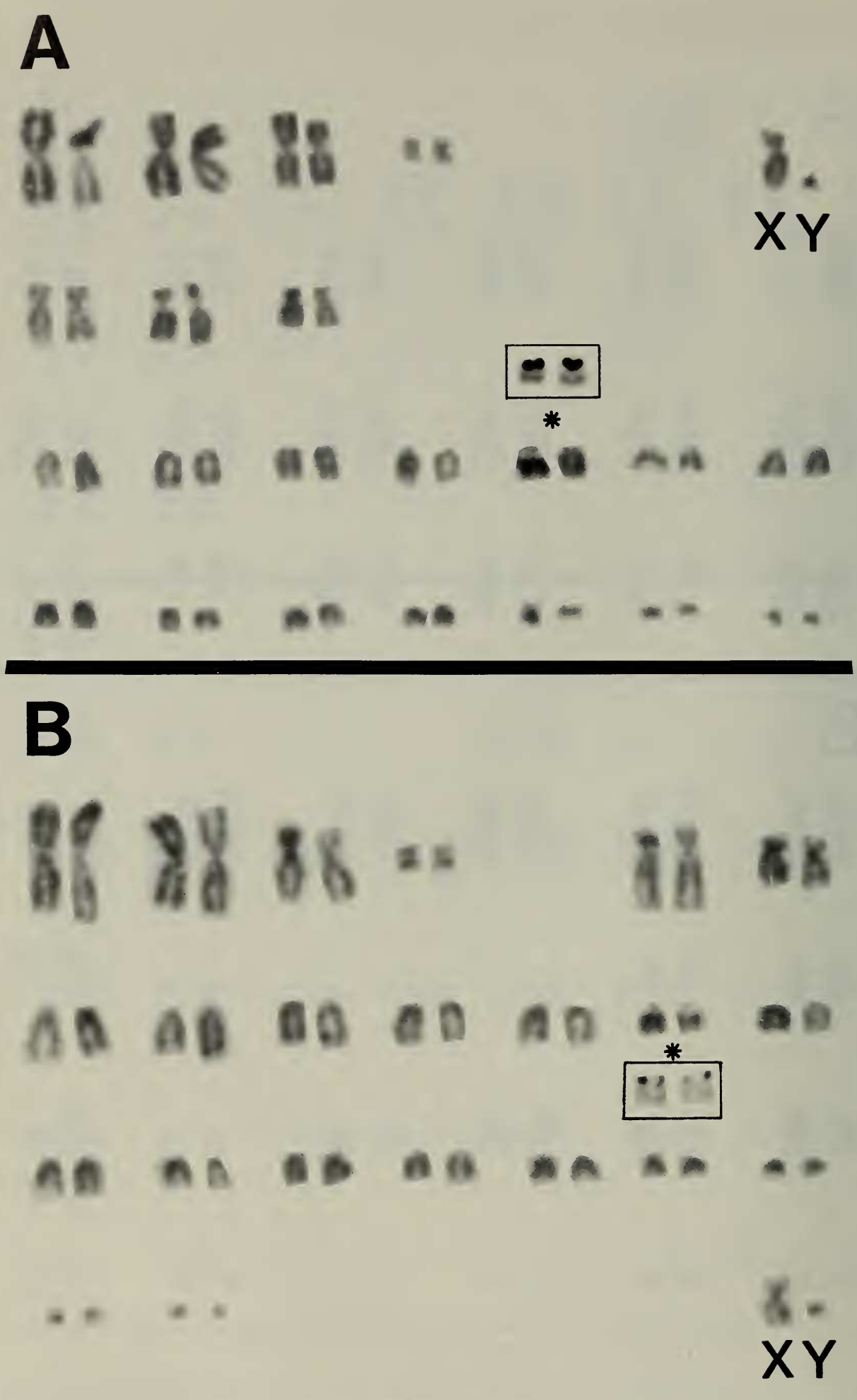

Fig. 3. Standard karyotypes and Ag-NORs (insets) of (A) *Ptenochirus jagori* ♂ (USNM 458322), 2N = 44, FN = 56(?); (B) *Ptenochirus minor* ♂ (USNM 458424), 2N = 46, FN = 56(?).

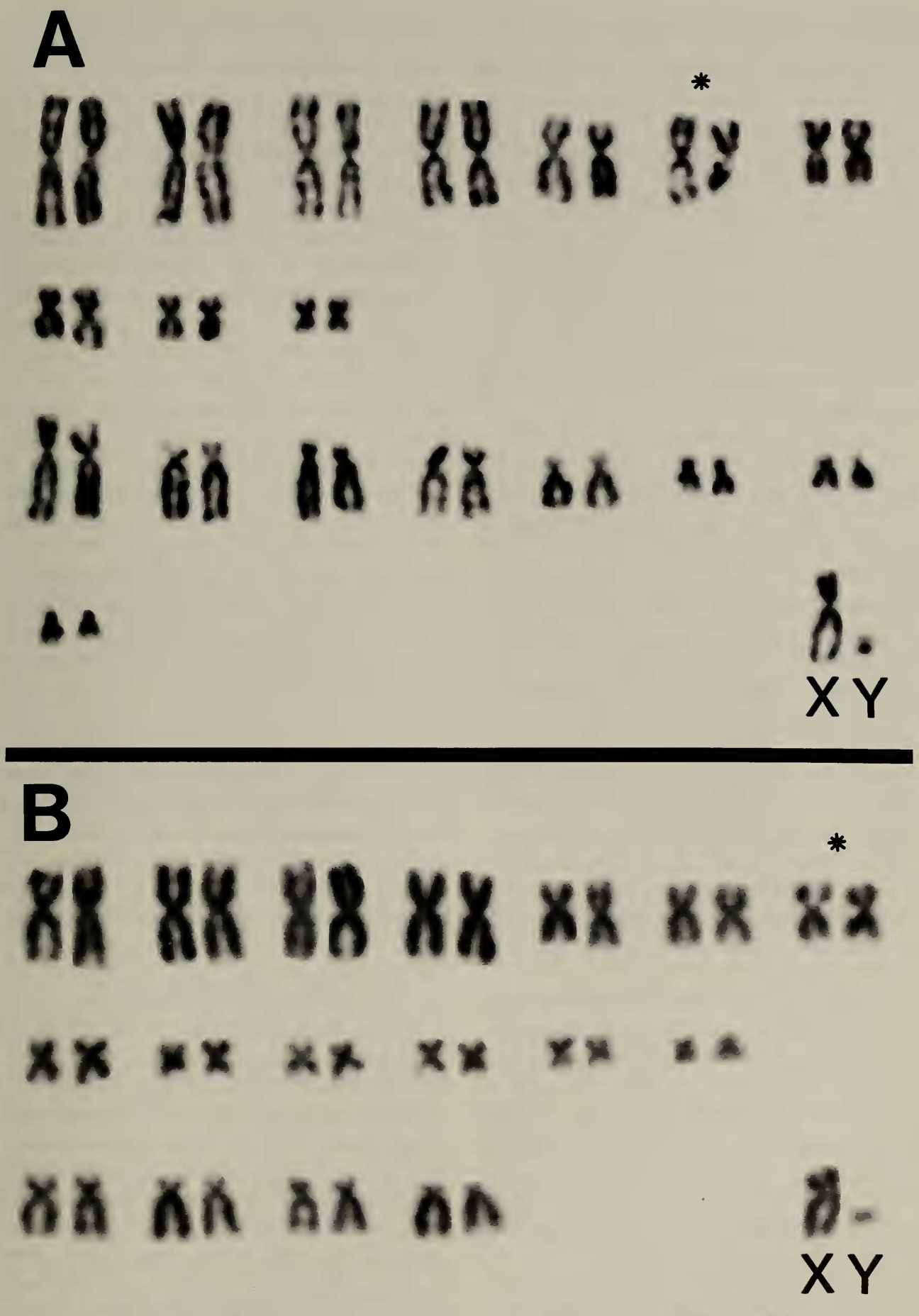

Fig. 4. Standard karyotypes of (A) *Pteropus hypomelanus* ♂ (USNM 458447), 2N = 38, FN = 72; (B) *Rousettus amplexicaudatus* ♂ (USNM 458486), 2N = 36, FN = 68. Asterisks indicate marker chromosomes.

guishable from those reported by previous workers (Yong et al. 1973, Ando et al. 1980, Harada & Kobayashi 1980). The autosomal complement consists of 11 pairs of metacentrics or submetacentrics, 2 pairs of subtelocentrics, and 3 pairs of acrocentric chromosomes. A pair of medium-sized metacentrics are marker chromosomes, that have a secondary constriction on the short arm near the centromere. In *C. brachyotis,* and in other species (see below), the secondary constriction coincides with the Ag-NOR site. The X chromosome is a medium-sized submetacentric and the Y, a small acrocentric.

Haplonycteris fischeri. 2N = 58, FN = 66(?), Fig. 1B.—The autosomal complement consists of 3 pairs of small to medium-sized submetacentrics, 2 pairs of small to medium-sized subtelocentrics, and 23 pairs of small to medium-sized acrocentric (or possibly subtelocentric) chromosomes. The marker chromosome is a medium-sized acrocentric. The X is a medium-sized submetacentric and the Y, a small acrocentric.

Harpyionycteris whiteheadi. 2N = 36, FN = 58, Fig. 2A.—The autosomal complement consists of six pairs of medium to large metacentric or submetacentric chromosomes, six pairs of medium-sized subtelocentrics, and five pairs of medium-sized acrocentrics. The marker chromosome is a large metacentric. The X chromosome is a medium-sized subtelocentric and the Y, a small acrocentric.

Nyctimene rabori. 2N = 38, FN = 60(?), Fig. 2B.—The autosomal complement consists of eight pairs of medium to large metacentrics and submetacentrics, four pairs of medium-sized subtelocentrics, and six pairs of small acrocentric (or subtelocentric) chromosomes. The marker chromosome is a medium-sized metacentric. The X chromosome is a medium-sized metacentric and the Y, a small submetacentric.

Ptenochirus jagori. 2N = 44, FN = 56(?), Fig. 3A.—The autosomal complement has 4 pairs of small to large metacentric or submetacentric chromosomes, 3 pairs of medium-sized subtelocentrics, and 14 pairs of small to medium-sized acrocentrics (or subtelocentrics). The marker chromosome is a medium-sized acrocentric. The X chromosome is a medium-sized submetacentric and the Y, a small acrocentric.

Ptenochirus minor. 2N = 46, FN = 56(?), Fig. 3B.—The standard karyotype is similar to that of the *P. jagori.* However the autosomal complement includes 2 subtelocentric pairs and 16 acrocentric pairs (as opposed to 3 and 14, respectively, for *P. jagori*).

Pteropus hypomelanus. 2N = 38, FN = 72, Fig. 4A.—A diploid number of 38 for this species was reported by Yong & Dhaliwal (1976), but the karyotype was not illustrated. The autosomal complement consists of 10 pairs of small to large metacentrics or submetacentrics, and 8 pairs of small to medium-sized subtelocentrics. The marker chromosome is a medium-sized submetacentric. The X chromosome is a medium-sized subtelocentric and the Y, a small acrocentric.

Rousettus amplexicaudatus. 2N = 36, FN = 68, Fig. 4B.—The autosomal group consists of 13 pairs of small to large metacentric and submetacentric chromosomes, and 4 pairs of medium-sized subtelocentrics. The marker chromosome is a medium-sized metacentric. The X is a medium-sized submetacentric and the Y, a small acrocentric.

Subfamily Macroglossinae

Eonycteris spelaea. 2N = 36, FN = 66, not figured.—Our specimens yielded karyotypes similar to those reported previously (Yong & Dhaliwal 1976, Ando et al. 1980, Harada et al. 1982). The autosomes consist of 14 pairs of small to large metacentrics or submetacentrics, 2 pairs of medium-sized subteocentrics, and 1 pairs of small acrocentrics. The marker chromosome is a medium-sized metacentric. The X is a medium-sized metacentric and the Y, a small submetacentric.

Macroglossus minimus. 2N = 34, FN = 62, not figured.—Our results agree with those of Ando et al. (1980) and Yong & Dhaliwal (1976). The autosomal complement includes 12 pairs of small to large metacentric and submetacentric chromosomes, 3 pairs of medium-sized subtelocentrics, and 1 pair of minute acrocentrics. The marker chromosome is a medium-sized metacentric. The X chromosome is a medium-sized metacentric and the Y, a small acrocentric.

Discussion

Karyotypic data represent a source of information that may be used for studies of phylogenetic relationships. Because our data and those of previous reports are, with a single exception (Haiduk et al. 1981), restricted to unbanded standard karyotypes, we believe that there is not yet an adequate basis for an independent analysis of relationships. Instead, we use Andersen's (1912) morphologically-based phylogeny as a framework in which to examine chromosomal data.

Andersen (1912) did not use current terminology in his monograph of the Pteropodidae. However, his general methodology is acceptable by today's standards. He differentiated character polarities, preferentially used derived characters in constructing the phylogeny, and recognized monophyly of groups. Andersen's (1912: pp. lii, lxi) graphic depiction of relationships within the portion of the subfamily Pteropodinae relevant to this study is shown in Fig. 5, with several slight modifications. First, he considered *Cynopterus* to be near or part of the ancestral stock that gave rise to other members of the *Cynopterus* group, and so placed *Cynopterus* at the base of the group rather than on a terminal branch. The arrangement shown represents our interpretation of his conclusions based on his discussion of characters. Second, we have included six genera that have been named since 1912. The genera *Aethalops, Latidens,* and *Paranyctimene* were described within the context of Andersen's character system, and their cladistic positions are unambiguous (Thomas 1932, Tate 1942, Thonglongya 1972). Unfortunately, the Philippine endemic genera *Alionycteris, Haplonycteris,* and *Otopteropus* were not described within Andersen's framework, so their positions are harder to determine. The three genera are very similar and undoubtedly closely related (Lawrence 1939; Kock 1969a, b). They resemble several other small cynopterines (e.g., *Aethalops* and *Balionycteris*), but most similarities involve character losses. Pending a thorough analysis of characters, we tenatively associate them with the *Cynopterus* group.

Several authors have differed with Andersen's interpretation of pteropodid phylogeny: these differences indicate areas of uncertainty. Miller (1907) and Simpson (1945) listed *Harpyionycteris* as the sole member of a separate subfamily Harpyionycterinae. Anderson himself recognized the subfamily in his formal classification. However, his discussion and diagrams indicate that he did so because of the many unique features of *Harpyionycteris,* and that he considered *Dobsonia,* a member of the rousettine section, to be its sister-taxon (Fig. 5). Similarly, Miller (1907), Simpson (1945), and others have recognized the unique features of *Nyctimene* and *Paranyctimene,* and have placed them in a separate subfamily. However, Andersen noted that *Nyctimene* shared derived characters with members of the cynopterine section, and he placed it in that group. Andersen considered most characters of *Myonycteris* to be primitive for the family. However, on the basis of several derived features he united this genus with the cynopterines. Bergmans (1976) transferred *Myonycteris* to the rousettine section based principally on characters that Andersen believed to be primitive for the family, but that Bergmans considered to be useful for defining the rousettines.

Previous karyotypic work on megachi-

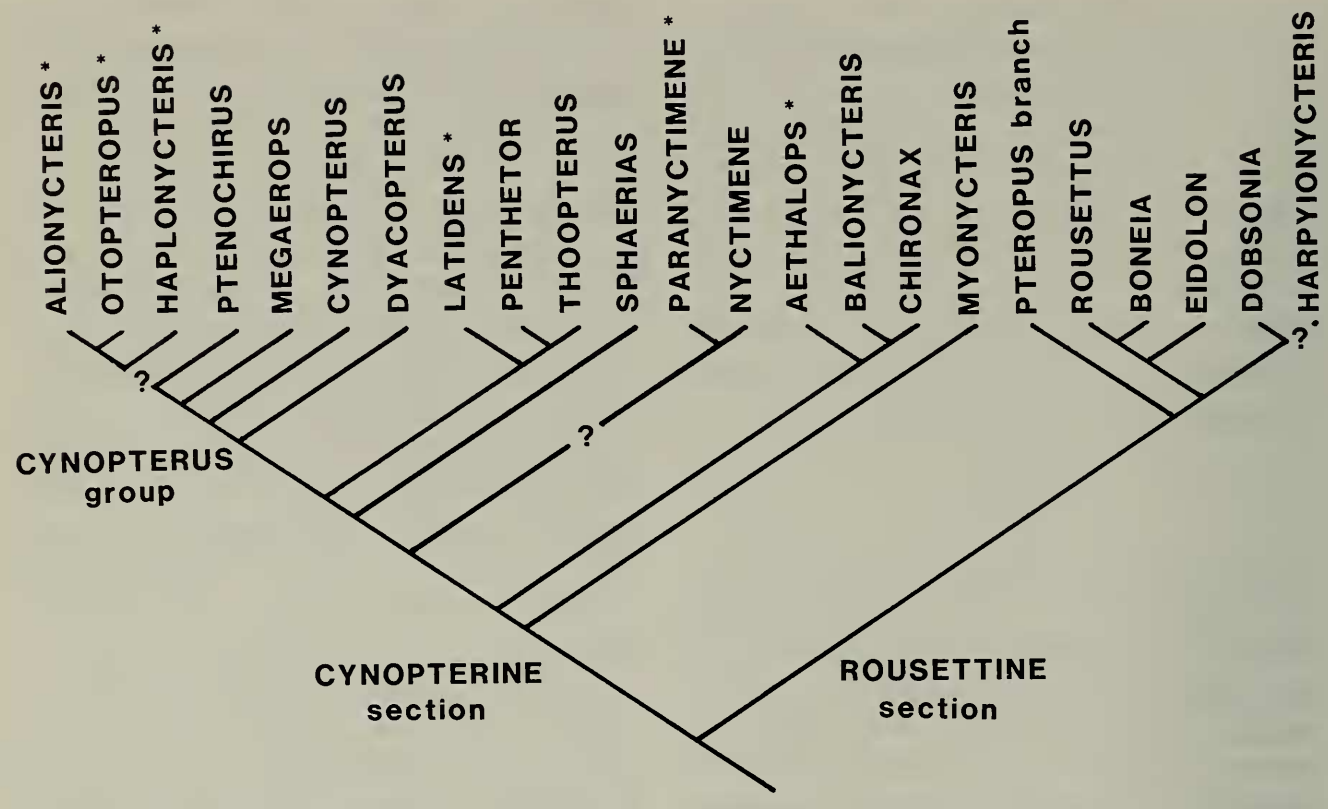

Fig. 5. Phylogeny of the cynopterine and rousettine sections of the subfamily Pteropodinae modified from Andersen (1912). Asterisks indicate genera described since 1912 (see text).

ropterans suggested a rather narrow range of variation in chromosome number and shape, most taxa having diploid numbers ranging from 34 to 38 and a majority of biarmed elements (summarized in Haiduk et al. 1980; 1981). Exceptions include *Balionycteris maculata* (2N = 24) and *Megaerops ecaudatus* (2N = 24, 26) with lower diploid numbers, and *Penthetor lucasi* (2N = 48) with a higher count (Yong & Dhaliwal 1976, Harada et al. 1982, Yong 1984). Our data on the Philippine endemic *Haplonycteris* (2N = 58; Fig. 1B) now place it at the upper extreme for the suborder Megachiroptera. In contrast to all other pteropodids examined except *Ptenochirus* (see below), the karyotype of *Haplonycteris* consists primarily of acrocentric elements. In contrast to *Cynopterus* (2N = 34; Fig. 1A), the FN differences (66 vs. 58) indicates a series of changes including both whole arm translocations and non-Robertsonian events.

The two species of *Ptenochirus,* another genus endemic to the Philippines, also have high diploid numbers (2N = 44 and 46). The difference in 2N supports the specific status of the recently described *P. minor* (Yoshiyuki 1979, Heaney & Rabor 1982). The species share an FN of 56 and appear to be separated by a single Robertsonian whole-arm translocation. As is the case with *Haplonycteris,* the karyotypes include a high proportion of acrocentrics (Fig. 3A, B). However, *Ptenochirus* also possess a number of large biarmed elements not present in *Haplonycteris.*

Andersen (1912) considered *Nyctimene* a specialized member of the cynopterine section. With FN = 60 and six pairs of small acrocentric elements, the standard karyotype of *Nyctimene rabori* (Fig. 2B) does resemble those of several cynopterines. However, the small metacentric marker chromosome and the metacentric Y distinguish it from other genera in this section.

The relationship of *Harpyionycteris* to other pteropodids is uncertain. Andersen (1912) associated it with his rousettine sec-

tion as the sister-taxon to *Dobsonia,* whereas Tate (1951) postulated a closer association with *Nyctimene* on the basis of certain shared characters (fusion of premaxillae and contact of lower canines). Although the diploid number of *Harpyionycteris* (2N = 38; Fig. 2A) is near the median value for the family (2N = 36), the standard karyotype is unique. Several pairs of relatively large acrocentric elements distinguish it from known karyotypes of epomophorine, rousettine and macroglossine genera. This feature allies it with the cynopterines, although the absence of small acrocentrics is distinguishing.

The rousettine section of the Pteropodinae seems relatively conservative karyotypically. All members of the genus *Pteropus* examined to date, including *P. hypomelanus* (Fig. 4A), exhibit similar standard karyotypes with 2N = 38, FN = 72 (Haiduk et al. 1980, Harada & Kobayashi 1980, Kasahara & Dutrilaux 1983). However, there are some interspecific differences in heterochromatin content (Kasahara & Dutrilaux 1983). *Rousettus* karyotypes resemble those of *Pteropus* in that they consist almost exclusively of biarmed elements. The standard karyotype of *Rousettus amplexicaudatus* (2N = 36, FN = 68; Fig. 4B) is indistinguishable from that reported by Harada et al. (1982) and Ray-Chaudhuri et al. (1968) for *R. leschenaulti.* The only other member of the genus that has been examined, *Rousettus aegyptiacus* (2N = 36, FN = 66), differs from *R. amplexicaudatus* and *R. leschenaulti* by a single rearrangement of the smallest autosomal element, which is acrocentric rather than biarmed (Dulić & Mutere 1973, Haiduk et al. 1981).

Our data on the widespread macroglossine species *Eonycteris spelaea* and *Macroglossus minimus* agree with previous findings (Yong and Dhaliwal 1976). Little karyotypic variation has been detected among macroglossines, but few taxa have been examined (Haiduk et al. 1980).

Extreme diploid numbers (24 to 58) for the pteropodids are confined to the cynopterine section of the subfamily Pteropodinae, whereas in the rousettine section and in the Macroglossinae, presumably outgroups to cynopterines, diploid numbers range only from 34 to 38 (Haiduk et al. 1980). This pattern suggests that both higher and lower diploid numbers represent derived states within the cynopterine section. The morphological specializations of both *Haplonycteris* and *Megaerops* relative to the presumed primitive genus *Cynopterus* (Andersen 1912; Lawrence 1939) support this contention. The broad range in FN (44–66) indicates that karyotypic evolution within the cynopterine section has involved more than Robertsonian rearrangements.

With the possible exception of *Scotonycteris ophiodon,* all pteropodids examined possess a pair of marker chromosomes with secondary constriction sites (Haiduk et al. 1980). Yong (1984) demonstrated that the secondary constriction corresponds to the silver-stained nucleolar organizer region in *Megaerops.* This same relationship, which also exists for several vespertilionids (Volleth 1987), was observed for all taxa in this study. In a few of our specimens, preparations consistently revealed only one marker/NOR element (e.g., Fig. 1B). No specimen had more than one pair. In *Haplonycteris* and *Ptenochirus,* the NOR sites are located on medium-sized acrocentrics. In the other genera, they are on a pair of medium-sized or large metacentrics or submetacentrics. For all taxa, the NORs are located interstitially near the centromere. The general uniformity of the marker arms suggests that they are homologous throughout the family. However, variation in the size of biarmed marker chromosomes (e.g., between *Harpyionycteris* and *Nyctimene*) may indicate non-homologous Robertsonian events or differences in heterochromatin content.

Data currently available allow us to draw several general conclusions. First, the subfamily Macroglossinae and the rouset-

tine section of the subfamily Pteropodinae exhibit low variability in gross chromosomal morphology. Second, our data reinforce earlier observations of the cynopterine section of the Pteropodinae as the most karyotypically variable clade in the family. Third, the karyotype of *Harpyionycteris* further highlights the uncertainty of its phylogenetic placement. Although these conclusions demonstrate the utility of karyotypes in investigating pteropodid phylogenetic relationships, they also indicate the need for more extensive studies involving banding data.

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